

New records of *Darevskia armeniaca* (Méhely, 1909) and *Darevskia valentini* (Boettger, 1892) (Squamata, Sauria, Lacertidae) from Armenia and updated geographic distribution maps

Varos G. Petrosyan,¹ Feodor A. Osipov,¹ Vladimir V. Bobrov,¹ Natalia N. Dergunova,¹ Felix D. Danielyan,² Marine S. Arakelyan²

1 A.N. Severtsov Institute of Ecology and Evolution of the Russian Academy of Sciences, Moscow 119071, Russia. **2** Department of Biology, Yerevan State University, Yerevan 555240, Armenia.

Corresponding author: Varos G. Petrosyan, petrosyan@sevin.ru



Abstract

During field survey in 2018, we recorded in Armenia the occurrences of the parthenogenetic lizard *Darevskia armeniaca* and its “paternal” bisexual species *D. valentini*. Based on our new data and records taken from publications and museums, we update the distribution maps of these species. The new records expand the geographical boundaries of sympatric habitats of these species and provide additional data for understanding the mechanisms of reticulate evolution and hybrid speciation.

Key words

Bisexual species, Reptilia, reticulate evolution, rock lizards, unisexual species.

Academic editor: Ross MacCulloch | Received 4 October 2018 | Accepted 20 December 2018 | Published 11 January 2019

Citation: Petrosyan VG, Osipov FA, Bobrov VV, Dergunova NN, Danielyan FD, Arakelyan MS (2019) New records of *Darevskia armeniaca* (Méhely, 1909) and *Darevskia valentini* (Boettger, 1892) (Squamata, Sauria, Lacertidae) from Armenia and updated geographic distribution maps. Check List 15 (1): 21–31. <https://doi.org/10.15560/15.1.21>

Introduction

In a book on rock lizards of the Caucasus, Darevsky (1967) reviewed all available information on their taxonomy and all known record sites for 8 species and 20 subspecies. Since that time, a great amount of data on rock lizards has been accumulated and published. Moreover, the lizards previously placed in the subgenus *Archaeolacerta* of the genus *Lacerta* were combined into the new genus *Darevskia* (Arribas 1999). Currently, this genus includes 33 species (AG Lacerta 2018). Most of them occur in the Caucasus region. Among these, 4 species are parthenogenetic (*Dareskia armeniaca* (Mehely, 1909), *D. dahli* (Darevsky, 1957), *D. rostombekowi*

(Darevsky, 1957) and *D. unisexualis* (Darevsky, 1966)) and all occur in Transcaucasia.

We present new data on the distribution in Armenia of 2 species, *D. armeniaca* (Mehely, 1909) and *D. valentini* (Boettger, 1892), which we collected during field studies conducted in 2018. Morphological, ecological, cytological, and genetic studies have shown that the parthenogenetic species *D. armeniaca* originated as a result of natural hybridization between the closely related bisexual species *D. mixta* (Méhely, 1909) (“maternal” species) and *D. valentini* (“paternal” species) (Darevsky 1967, Darevsky and Danielyan 1968, Uzzell and Darevsky, 1975, Moritz et al. 1992, MacCulloch et al. 1995, Murphy et al. 1996, Fu et al. 2000).

Methods

We collected data on the distribution of *D. armeniaca* and *D. valentini* from museum records and published literature. The museum specimens were from the Zoological Museum of M.V. Lomonosov Moscow State University (ZMMU), the Museum of Zoological Institute, Russian Academy of Sciences (ZISP), and the Royal Ontario Museum, Toronto, Canada (ROM). ROM data are published in the Global Biodiversity Database (*D. armeniaca*: GBIF occurrence data <https://doi.org/10.15468/dl.pzhflc>; *D. valentini*: GBIF occurrence data <https://doi.org/10.15468/dl.howz7o>). We also analyzed and digitized data published in papers from 1967 to 2017. We found 98 publications on *D. armeniaca* and 85 on *D. valentini* for Armenia, Georgia, Azerbaijan, and Turkey. After analyzing the data on the locations of 2,148 individuals, we selected only those record sites of the species that contained information about the species identification and geographic coordinates. All localities with geographic coordinates and elevations are in the Appendix. General characteristics of the species record sites from museum and literature sources are presented in Table 1.

Field studies were conducted in Armenia and Nagorno-Karabakh (“Artsakh”) in July 2018 along the following route: Tsaghkadzor (July 6–7); Lchashen, Lychan, Hayravank, Hankavan (July 8); Sevanavank, Dilijan National Park, Haghartsin, Goshavank, Hrazdan (July 9); Tsovak, Sotk, Nagorno-Karabakh (near Zuar)(July 10); Kuchak (Kutchak) (July 11); KhorVirap, Noravank, Yeghegnadzor, Hors (July 12); Hors conservation area (July 12–14); Amberd (July 14); Harichavank, Mets Sepasar, Arpi-Spitak (July 15); Gogaran (July 16); Marmashen (July 17); Gyumri vicinity (July 22–24). During this time, active work was carried out to find new localities and update existing data on the geographical distribution of *Darevskia* in Armenia. Special attention was paid to the zones of sympatry of the studied species. As a result, 68 locations of rock lizards were recorded, and our data included a detailed description of biotopes and abiotic environmental parameters. Each site was examined for about 1 hour to record lizard presence. The survey was conducted during sunny windless morning hours to reduce the influence of weather

on the activity of lizards. The geographical coordinates (C_{long} , C_{lat}) and elevation (H_E) of each site were determined using a Garmin Montana 680t GPS receiver (Garmin Corp., Olathe, KS, USA). Biotopes were described in terms of rock sizes, vegetation type, and landscape conditions. Temperature (T_A) and humidity (W_A) were measured with an AZ811 professional hygrometer (AQUA-LAB, Moscow, Russia). Temperature of the underlying surface of rocks (T_{US}), stones, and soil was measured with a KL-98501 probe (OOO LANFOR RUS, St. Petersburg, Russia). Wind speed (V_W) was measured with a Smart sensor DA09 anemometer (NGO Measuring Instruments, Moscow, Russia).

Specimens were captured by noose. Captured lizards were photographed (anterolateral surface and temporal areas of the head and the anal area) with a Nikon Coolpix B500 digital camera (Nikon Corporation, Tokyo, Japan) to enable their identification. The sex of captured individuals was determined by visual inspection. Male and female rock lizards are easily distinguished by enlarged femoral pores on the ventral region of the hind legs in males. The males also have larger heads and brighter colors as well as deep blue markings along the side of their belly. In doubtful cases, a lizard may be probed to determine presence of hemipenes without harming it. Specimens were released at the point of capture immediately after examination. Fieldwork was carried out under a Scientific Purposes Permit from the Ministry of Nature Protection of the Republic of Armenia Code 5/22.1/51043 for activities pertaining to the capture, handling, and/or collection of wild animals for scientific purposes, including Armenian–Russian collaborative projects. All voucher photographs are deposited in the research collection of the Institute of Ecology and Evolution of the Russian Academy of Sciences (IEERAS).

We used our new field records, museum records, and published data to create a database of occurrences for the 2 species, which was mapped using ArcGIS Desktop 10.4.1. The base maps for Armenia, Georgia, Azerbaijan, and Russia were obtained from Open Street Map (<https://www.openstreetmap.org>), and for Turkey and Iran, we used data from Natural Earth (<https://www.naturalearth-data.com/>).

Table1. General characteristics of the species record sites.

Sources	Species	No. of records	Species identification	References
ROM & published data	<i>D. armeniaca</i>	29	Analysis of allozyme loci, analysis of mt-DNA, morphological features	MacCulloch et al. 1995, Murphy et al. 1996, Fu et al. 1999, 2000
ZISP & published data	<i>D. armeniaca</i>	60	Morphological characteristics, analysis of allozyme loci	Darevsky 1966, 1967, Darevsky and Danielyan 1968, Uzzell and Darevsky 1975
Original data published up to 2018	<i>D. armeniaca</i>	109	Multilocus DNA fingerprinting (mini and microsatellite markers), morphological features	Tokarskaya et al. 2001, Martirosyan et al. 2003, Petrosyan et al. 2003, Malysheva et al. 2007, Arakelyan et al. 2011
ROM & published data	<i>D. valentini</i>	64	Analysis of biochemical markers, morphological features	Uzzell and Darevsky 1975, Darevsky 1967, 1968
Original data published up to 2018	<i>D. valentini</i>	46	Chromosomal analysis, DNA fingerprinting (minisatellite markers), morphological features	Danielyan et al. 2008a, 2008b, Arakelyan et al. 2011

Results

Darevskia armeniaca (Mehely, 1909)

New records. During the field survey of 2018, we caught and identified 35 individuals in 18 localities. The lizards were observed by VGP, FAO, VVB and MSA.

All Armenia. **1:** Kotayk Province, Tsaghkadzor (40°32'7" N, 044°42'30" E, 1917 m elev.); 1 female; 6 July 2018, IEERAS 366. **2:** Gegharkunik Province, Lchashen (40°30'39" N, 044°56'08" E, 1950 m elev.); 1 female; 8 July 2018, IEERAS 367. **3:** Kotayk Province, Meghradzor (40°35'49" N, 044°38'51" E, 1833 m elev.); 1 female; 8 July 2018, IEERAS 369. **4:** Kotayk Province, YSU student camp (40°36'40" N, 044°34'39" E, 1832 m elev.); 1 female; 8 July 2018, IEERAS 370. **5:** Kotayk Province, YSU student camp (40°36'43" N, 044°34'35" E, 1830 m elev.); 1 female; 8 July 2018, IEERAS 371. **6:** Kotayk Province, Tutudzhyur (40°38'11" N, 044°32'21" E, 1917 m elev.); 1 female; 8 July 2018, IEERAS 372. **7:** Kotayk Province, Ehribuni camp (40°37'14" N, 044°28'6" E, 2088 m elev.); 2 females; 8 July 2018, IEERAS 373. **8:** Tavush Province, Semyonovsky Mountain Pass (40°41'41" N, 044°51'16" E, 1578 m elev.); 7 females; 9 July 2018, IEERAS 374. **9:** Tavush Province, road to Dilijan (40°44'2" N, 044°49'4" E, 1342 m elev.); 1 female; 9 July 2018, IEERAS 375. **10:** Tavush Province, Haghartsin (40°48'3" N, 044°53'17" E, 1443 m elev.); 10 females; 9 July 2018, IEERAS 376. **11:** Tavush Province, Haghartsin Monastery (40°48'7" N, 044°53'26" E, 1436 m elev.); 1 female; 9 July 2018, IEERAS 377. **12:** Kotayk Province, Kentron-Hrazdan (40°30'23" N, 044°44'56" E, 1700 m elev.); 1 female; 9 July 2018, IEERAS 378. **13:** Gegharkunik Province, Karabakh–Sotk road (40°13'23" N, 046°0'4" E, 2124 m elev.); 1 female; 10 July 2018, IEERAS 379. **14:** Aragatsotn Province, Kuchak (40°31'44" N, 044°23'18" E, 1920 m elev.); 1 female; 11 July 2018, IEERAS 381. **15:** Vayots Dzor Province, Hors (39°51'31" N, 045°11'44" E, 2080 m elev.); 1 female; 13 July 2018, IEERAS 383. **16:** Shirak Province, Harichavank (40°36'23" N, 043°59'59" E, 1993 m elev.); 2 females; 15 July 2018, IEERAS 384. **17:** Shirak Province, Mets Sepasar (41°01'49" N, 043°49'18" E, 1990 m elev.); 1 female; 15 July 2018, IEERAS 385. **18:** Shirak Province, Mets Sepasar bridge (41°1'49" N, 043°49'15" E, 1986 m elev.); 1 female; 15 July 2018, IEERAS 387.

We collected 1–10 specimens at each site. The above localities had been previously documented but without describing key abiotic environmental factors (Appendix Table A1). We recorded lizard occurrence in anthropogenic habitats (stone bridges, walls of churches, stone slabs of cemeteries, human settlements, and highways with stone embankments in the mountains) at 14 sites (Figs 1–4). Four record sites were located on outcrops of rocks, boulders, large stones, and clay cliffs in the mountain steppes, mountain meadows, mountain forests, and the subalpine zone of the central and eastern parts of Armenia. We examined all the biotopes where *D. armeniaca* could likely occur.



Figure 1. A. *Darevskia armeniaca* on a stone fence along the highway within the city of Tsaghkadzor, Kotayk Province, 6 July 2018. B. Close-up of the lizard. Photographs by FAO.



Figure 2. Rock outcrops on the slope of the Gegham mountains, Lchashen, Gegharkunik Province, 8 July 2018. Photograph by FAO.



Figure 3. Sevanavank Monastery on the shore of Lake Sevan, Gegharkunik Province, 9 July 2018. Photograph by FAO.

Figure 5 shows an updated map using our new records, plus data from the literature and museum sources.

Identification. *Darevskia armeniaca* was identified using species identification guide in Darevsky (1967). Figure 6 shows distinguishing features of this species. All captured individuals were found to be females, determined by visual inspection of the genitals.

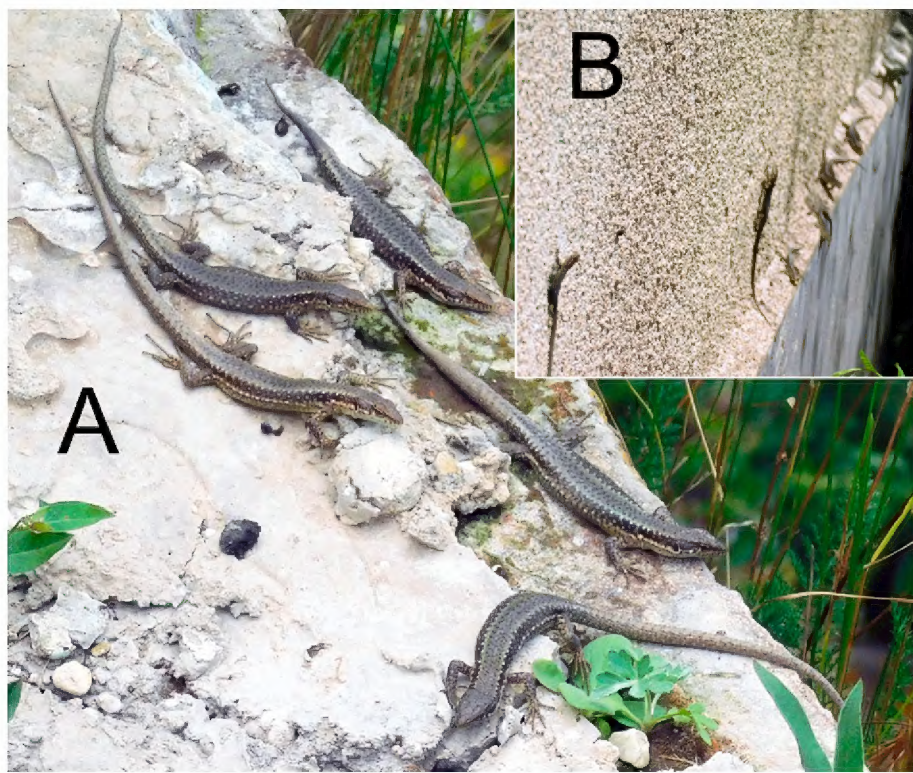


Figure 4. Groups of *Darevskia armeniaca* in urban areas. **A.** At a bridge over the river in Lake Arpi National Park, near the village of Mets Sepasar, Shirak Province, 15 July 2018. **B.** A wall of a residential house in Semyonovsky Mountain Pass, Tavush Province, 9 July 2018. Photographs by FAO.

***Darevskia valentini* (Boettger, 1892)**

New records. During our field survey we captured and identified 11 individuals in eight localities. The lizards were observed by VGP, FAO, VVB and MSA.

All Armenia. **1:** Gegharkunik Province, Lchashen (40°30'39" N, 044°56'8" E, 1950 m elev.); 1 female; 8 July 2018, IEERAS 368. **2:** Gegharkunik Province, Karabakh–Sotk road (40°13'23" N, 046°0'4" E, 2124 m elev.); 1 female, 1 male; 10 July 2018, IEERAS 380. **3:** Aragatsotn Province, Kuchak (40°31'43" N, 044°23'18" E, 1920

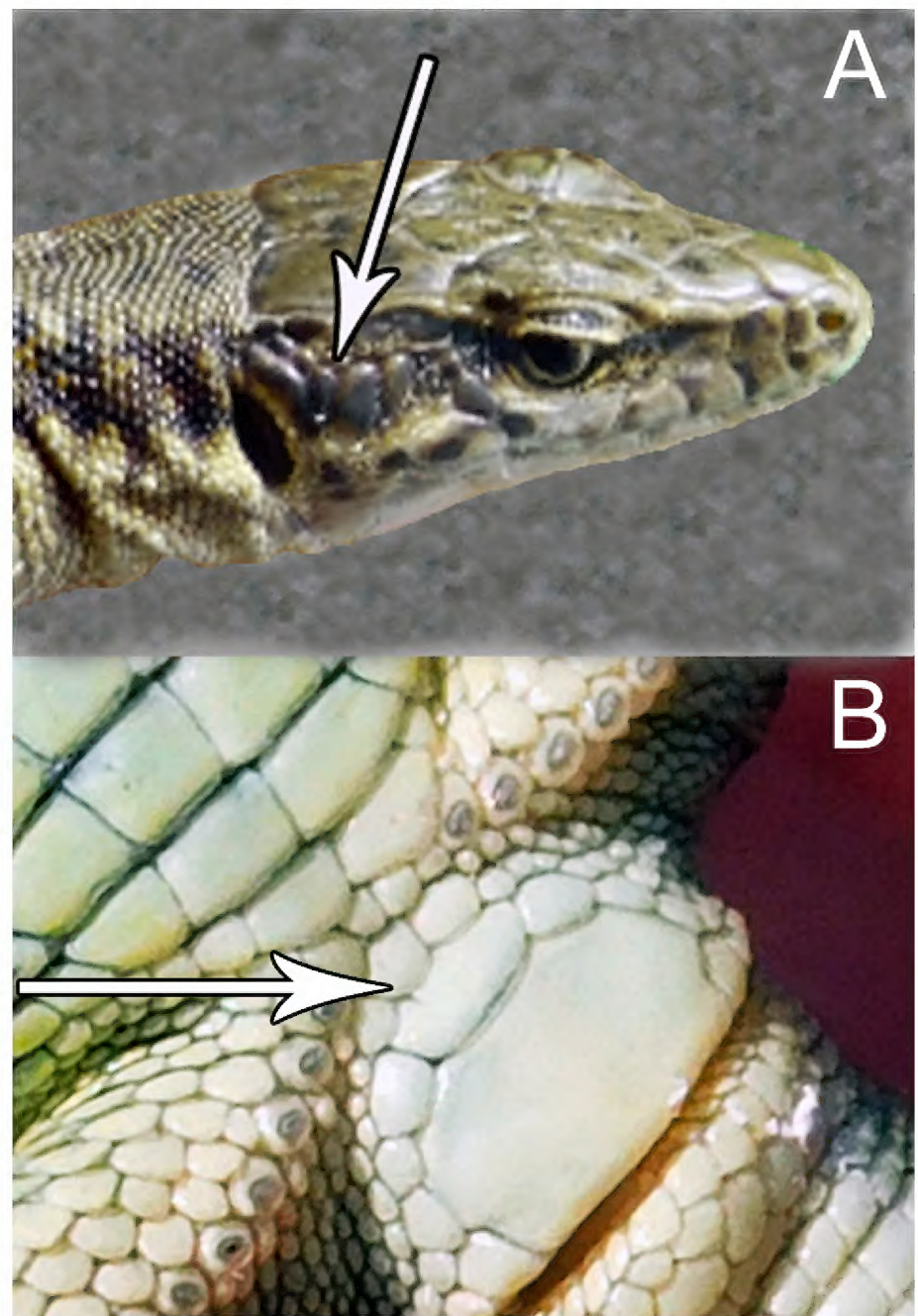


Figure 6. Distinguishing characters of *D. armeniaca*. **A.** Between the central temporal and tympanum shields are 2 scales of similar sizes or the central temporal shield touches the tympanic scale (indicated by arrow). **B.** In front of the large anal shield, there are 1 or 2 enlarged preanal scales of different size than the other preanals (indicated by arrow). Photographs by FAO.

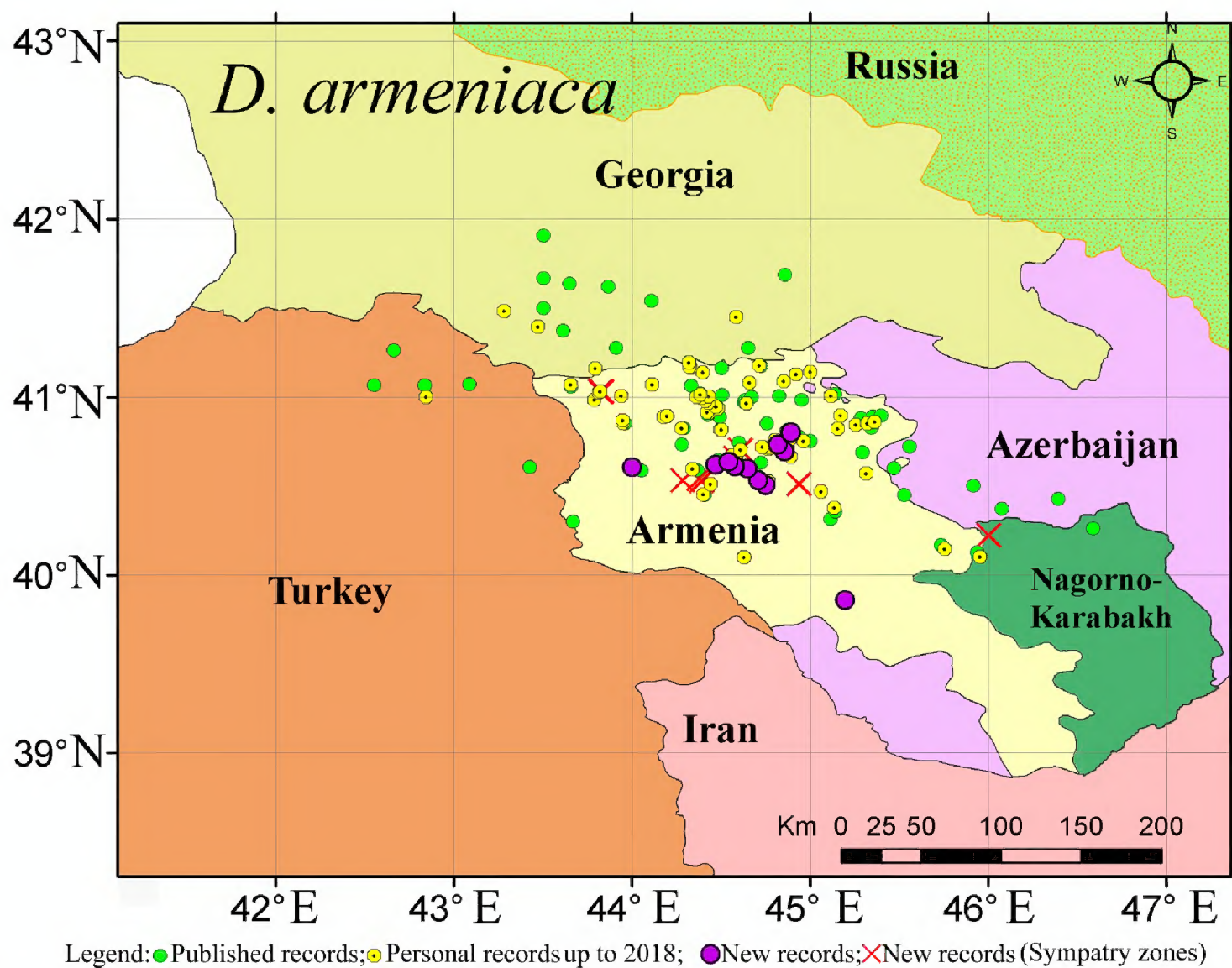


Figure 5. Geographical distribution of *Darevskia armeniaca* in Transcaucasia and Asia Minor based on our new records, museum and literature records (see Appendix).



Figure 7. Zone of sympatry of parthenogenetic species *D. armeniaca* (A) and its parental bisexual species *D. valentini* (B). Bridge over the river in Lake Arpi National Park, vicinity of Mets Sepasar, Shirak Province, 15 July 2018. Photograph by FAO.



Figure 8. Bridge over the river in Lake Arpi National Park, vicinity of Mets Sepasar, Shirak Province, 15 July 2018. Photograph by FAO.

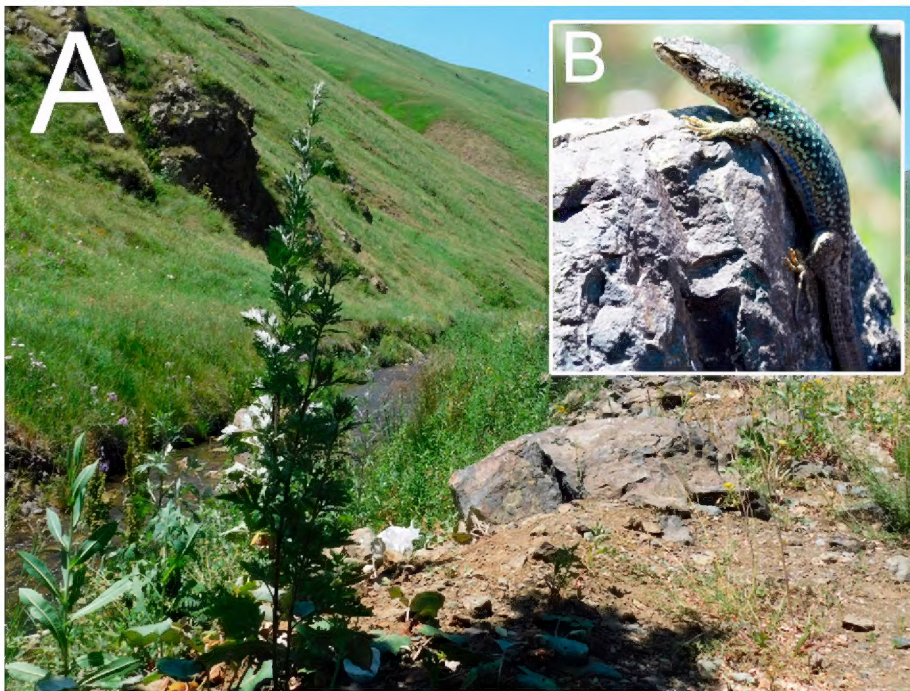


Figure 9. A. Heaps of stones along a creek in the foothills on the border of Armenia with Nagorno-Karabakh Gegharkunik Province. B. *Darevskia valentini* on the rocks in this habitat, 10 July 2018. Photographs by FAO.

m elev.); 1 male; 11 July 2018, IEERAS 382. **4:** Aragatsotn Province, Kuchak (40°31'44" N, 044°23'15" E, 1925 m elev.); 1 female; 19 July 2018, IEERAS 404. **5:** Aragatsotn Province, Kuchak (40°31'43" N, 044°23'23" E, 1916 m elev.); 1 male; 19 July 2018, IEERAS 405. **6:** Shirak Province, Mets Sepasar (41°01'49" N, 043°49'18" E, 1990

m elev.); 1 female; 15 July 2018, IEERAS 386. **7:** Shirak Province, Mets Sepasar (41°01'49" N, 043°49'17" E, 1990 m elev.); 1 female; 15 July 2018, IEERAS 406. **8:** Shirak Province, Mets Sepasar bridge (41°01'49" N, 043°49'15" E, 1986 m elev.); 3 females; 15 July 2018, IEERAS 388.

These localities were previously documented, but without describing specifying geographic coordinates and key abiotic environmental factors. We describe these factors in Appendix Table A1. One individual was captured at each site. The record sites are located in zones of sympatric occurrence of the paternal species *D. valentini* with the parthenogenetic *D. armeniaca* (Fig. 7). All the record sites were located on stone bridges along highways, on large stones, and clay cliffs in the mountain-steppe, mountain-meadow subalpine zone of the northern and eastern parts of Armenia and on the border with Nagorno-Karabakh. Some lizard habitats are shown in Figures 8 and 9.

Figure 10 is an updated distribution map using our new records, as well as literature and museum sources.

Identification. *Darevskia valentini* was identified using species identification guide in Darevsky (1967). Figure 11 shows distinguishing features of this species.

Discussion

The records of *D. armeniaca* indicated that this species is distributed rather widely in the Caucasus in northwestern Armenia, western Azerbaijan, and southern Georgia. It was also recorded in the valleys of the Trabzon, Ardahan and Kars in northeastern part of Turkey (Fig. 5). The data indicate that the geographic range of *D. valentini* is divided into several large isolated zones in the steppe highland and mountain-steppe zones of Armenia, Nagorno-Karabakh, southern Georgia, and eastern Turkey (Darevsky 1967) (Fig. 10).

The extensive areas where *D. armeniaca* occurs

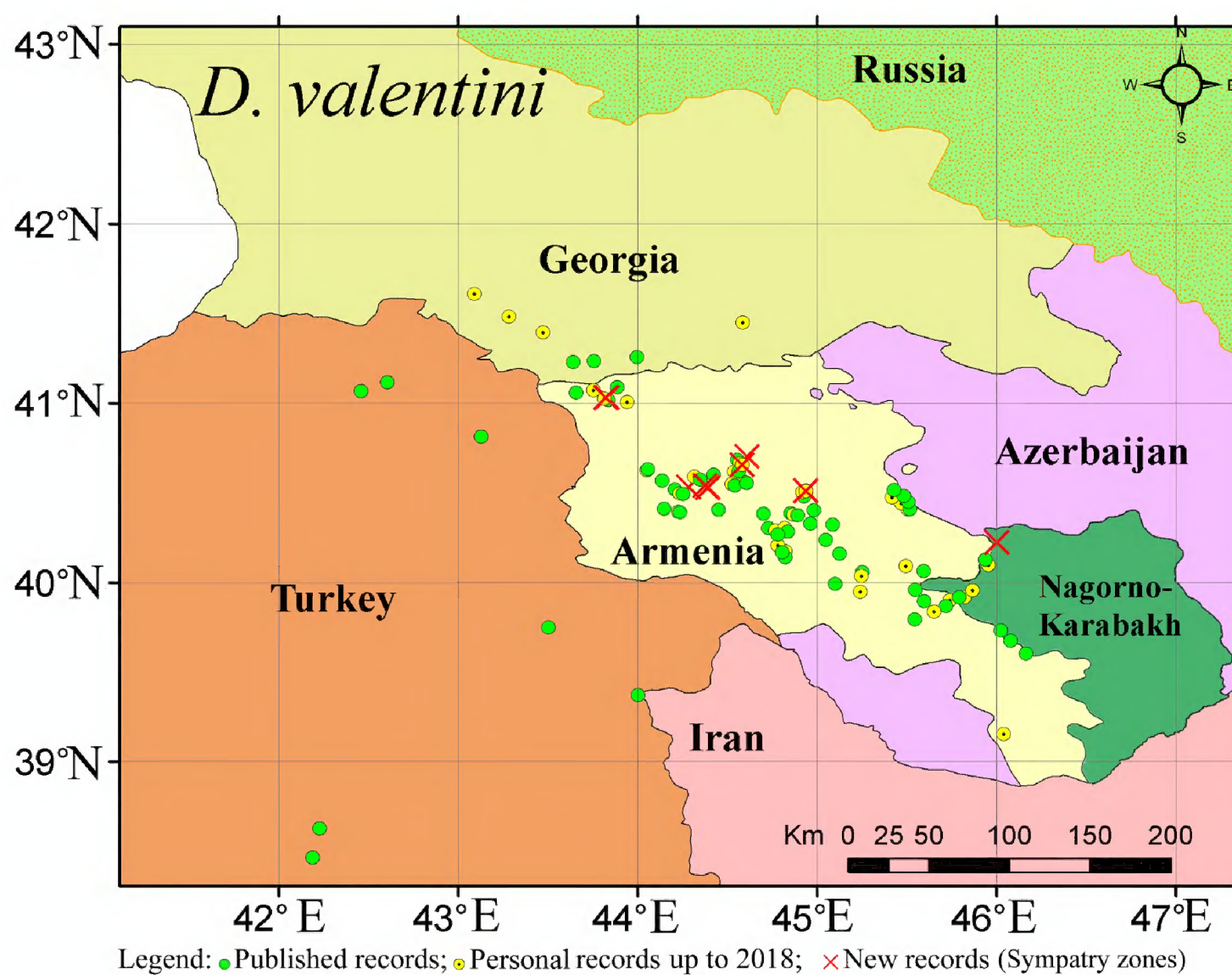


Figure 10. Geographical distribution of *D. valentini* in Transcaucasia and Asia Minor based on our new records, museum records and literature data (see Appendix).

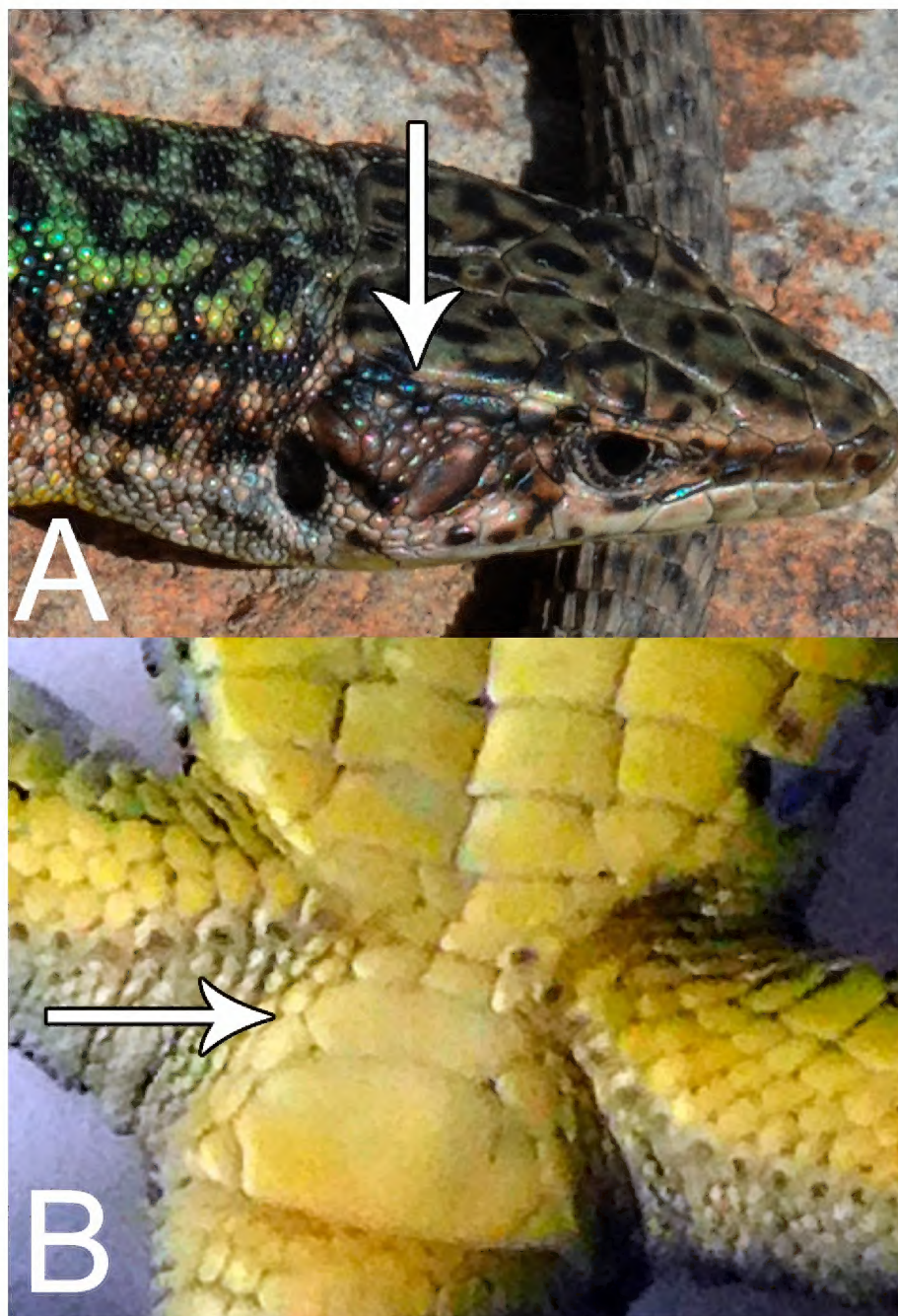


Figure 11. Distinguishing characters of *D. valentini* (male individual on the photographs). **A.** Group of small scales between the central temporal and tympanum shields (indicated by arrow). **B.** Single or sometimes double enlarged preanal scale (indicated by arrow). Photographs by MSA.

are located in the subalpine zone of the Gegham mountains and extends to the shores of Lake Sevan, the subalpine region of Mount Aragats, the north-western part of Armenia, and the adjacent areas of southern Georgia. Additionally, this species is reported in the subalpine zones of the Karabakh highland within the territory of Nagorno-Karabakh. Outside of the Caucasus, *D. armeniaca* is recorded in the eastern part of Turkey.

Most of the records were known from earlier studies, but we were able to verify the presence of both *D. armeniaca* and *D. valentini* in anthropogenic habitats such as along highways, in human settlements, on rock slabs in cemeteries, on walls of churches, and on stone bridges. Previously published data on the distribution of these species were updated with the addition of geographic coordinates and data on key abiotic environmental factors. Moreover, the geographical coordinates of the zones of sympatry were established.

The new records expand and clarify geographic distribution of the daughter and parental species in the sympatry zones. This is extremely important for understanding reticular evolution and hybrid speciation (Borkin and Darevsky 1980, Vasiliev 1985, Moritz 1991). Our data indicate that the elevation of the sympatry zones inhabited by *D. valentini* and *D. armeniaca* are intermediate between the habitat elevations for individual species occurrence; that is, the zones of sympatry are between the upper boundaries of the habitats of *D. armeniaca* and the lower boundaries of *D. valentini*.

Our comprehensive analysis of museum collections, GBIF, and published data show that false or ambiguous

records are common because of name changes, and obscure localization of sites without specifying geographical coordinates. The latter can lead to misinterpretation of geographic data. We found that the standard descriptions of native ranges of *D. valentini* and *D. armeniaca*, which are often simply repeated in the literature, may be deceptive. For this reason, there is a need for field surveys for the updating of the distribution patterns of lizard species to reveal the mechanisms of their reticular evolution in the past, present, and future. These data can be valuable for environmental protection agencies to preserve the most important habitats of these species.

Acknowledgements

The study was supported by the Russian Foundation for Basic Research, Project No. 17-00-00427. We are grateful to V.F. Orlova, E.A. Galoyan (Zoological Museum of Moscow State University) and N.B. Ananjeva (Zoological Institute, Russian Academy of Sciences) for their assistance in studies of lizard museum specimens. We also would like to thank I.Y. Feniova (A.N. Severtsov Institute of Ecology and Evolution, Russian Academy of Sciences) who helped with English. This manuscript was greatly improved by comments from the academic editor, Ross MacCulloch.

Authors' Contributions

VGP collected the data in the field, created the database, made the literature review, and wrote the text; FAO collected the data in the field, analyzed literature data, took the photographs, and revised the text; VVB collected the data in the field, analyzed museum specimens, identified the species, and revised the text; NND prepared the maps, and revised the text; FDD and MSA collected the data in the field, made the literature review, established of geographical coordinates, and revised the text.

References

AG Lacertiden (2018) Arbeitsgemeinschaft Lacertiden. <http://www.lacerta.de/AS/AGLacertiden1.php?Lang=eng>. Accessed on: 2018-12-30.

Arakelyan MS, Danielyan FD, Corti C, Sindaco R, Leviton AE (2011) Herpetofauna of Armenia and Nagorno-Karabakh. SSAR Publications, Salt Lake City, 154 pp.

Arribas OJ (1999) Phylogeny and relationships of the mountain lizards of Europe and Near East (*Archaeolacerta* Mertens, 1921, sensu lato) and their relationships among the Eurasian lacertid radiation. Russian Journal of Herpetology 6 (1): 1–22.

Borkin LJ, Darevsky IS (1980) Reticular (hybridogeneous) speciation in vertebrate. Zhurnal Obshchei Biologii 41 (4): 485–506 [in Russian].

Danielyan F, Arakelyan M, Stepanyan I. (2008a) The progress of microevolution in hybrids of rock lizards of genus *Darevskia*. Biological Journal of Armenia 60 (1–2): 147–156.

Danielyan F, Arakelyan M, Stepanyan I. (2008b) Hybrids of *Darevskia valentini*, *D. armeniaca* and *D. unisexualis* from sympatric population in Armenia. Amphibia-Reptilia 29: 487–504. <https://doi.org/10.1163/156853808786230424>

Darevsky IS (1966) Natural parthenogenesis in a polymorphic group of Caucasian rock lizards related to *Lacerta saxicola* Eversmann. Journal of the Ohio Herpetological Society 3: 115–152.

Darevsky IS, Danielyan FD (1968) Diploid and triploid progeny arising from natural mating of parthenogenetic *Lacerta armeniaca* and *L. unisexualis* with bisexual *L. saxicola valentini*. Journal of Herpetology 2 (3/4): 65–69. <http://doi.org/10.2307/1563104>

Darevsky IS (1967) Rock Lizards of the Caucasus: Systematics, Ecology and Phylogenesis of the Polymorphic Groups of Caucasian Rock Lizards of the Subgenus *Archaeolacerta*. Leningrad, Nauka Press, 214 pp. [in Russian].

Fu J, Murphy RW, Darevsky IS (1999) Limited genetic variation in *Lacerta mixta* and its parthenogenetic daughter species: evidence from cytochrome b and AT Phase 6 gene DNA sequences. Genetica 105 (3): 227–231.

Fu J, MacCulloch RD, Murphy RW, Darevsky IS (2000) Clonal variation in the Caucasian rock lizard *Lacerta armeniaca* and its origin. Amphibia-Reptilia 21 (1): 83–89.

MacCulloch RD, Murphy RW, Kupriyanova L.A, Darevsky IS, Danielyan FD (1995) Clonal variation in the parthenogenetic rock lizard *Lacerta armeniaca*. Genome 38 (6): 1057–1060.

Martirosyan IA, Kan NG, Malysheva DN, Trofimova AA, Korochkin LI, Ryskov AP, Tokarskaya ON, Petrosyan VG, Danielyan FD, Darevskii IS (2003) Variation of mini- and microsatellite DNA repeats in parthenogenetic lizard *Darevskia armeniaca* as revealed by DNA fingerprinting analysis. Russian Journal of Genetics 39 (2): 159–165.

Moritz C (1991) The origin and evolution of parthenogenesis in *Heteronotia binoi* (Gekkonidae): evidence for recent and localized origin of widespread clones. Genetics 129: 211–219.

Moritz C, Uzzell T, Spolsky C, Horts H, Darevsky I, Kupriyanova L, Danielyan F (1992) The maternal ancestry approximate age of parthenogenetic species of Caucasian lizards (*Lacerta*: Lacertidae). Genetica 87: 53–62.

Murphy R, Darevsky I, MacCulloch R, Fu J, Kupriyanova L. (1996) Evolution of the bisexual species of Caucasian rock lizards: a phylogenetic evaluation of allozyme data. Russian Journal of Herpetology 3: 18–31.

Petrosyan VG, Tokarskaya ON, Malysheva DN, Ryskov AP (2003) Quantitative assessment of gene diversity and between-population differentiation of parthenogenetic lizard of the genus *Darevskia* using mini- and microsatellite DNA markers. Russian Journal of Genetics 39 (10): 1201–1207.

Tokarskaya ON, Kan NG, Petrosyan VG, Martirosyan IA, Grechko VV, Danielyan FD, Darevsky IS, Ryskov AP (2001) Genetic variation in parthenogenetic Caucasian rock lizards of the genus *Lacerta* (*L. dahli*, *L. armeniaca*, *L. unisexualis*) analyzed by DNA fingerprinting. Molecular Genetics and Genomics 265 (5): 812–819.

Uzzell T, Darevsky IS (1975) Biochemical evidence for the hybrid origin of the parthenogenetic species of *Lacerta saxicola* complex (Sauria, Lacertidae) with a discussion of some ecological and evolutionary implications. Copeia 2: 204–222.

Vasiliev VP (1985) Evolutionary Karyology of Fish. Nauka, Moscow, 300 pp. [In Russian].

Appendix

Geographical coordinates and elevations of published and personal records up to 2018 for *Darevskia armeniaca* and *D. valentini*.

D. armeniaca (latitude, longitude), elevation, country, province, reference, sources. (40.7450, 44.8200), 1443 m, Armenia, Tavush, (Murphy et al. 1996), published data; (40.6469, 44.4816), 2108 m, Armenia, Ankavan, (Murphy et al. 1996), published data; (40.6375, 44.5483), 2070 m, Armenia, Ankavan, (Murphy et al. 1996), published data;

(40.6375, 44.5483), 2070 m, Armenia, Ankavan, (Fu et al. 1999), published data; (40.7440, 44.8280), 1370 m, Armenia, Tavush, (Murphy et al. 1996), published data; (40.6910, 44.8580), 1614 m, Armenia, Tavush, (Murphy et al. 1996), published data; (41.5000, 43.5000), 1681 m, Georgia, Samtskhe-Javakheti, (Fu et al. 1999), published data; (40.6890, 44.8560), 1705 m, Armenia, Tavush, (Darevsky 1967), published data; (41.0180, 44.3800), 1409 m, Armenia, Lori, (Murphy et al. 1996), published data; (40.7250, 44.7890), 1613 m, Armenia, Tavush, (Murphy et al. 1996), published data; (41.6867, 44.8556), 439 m, Armenia, Tavush, (Darevsky 1967), published data; (40.7454, 44.8553), 1355 m, Armenia, Tavush, (Darevsky 1967), published data; (40.6109, 44.5643), 2019 m, Armenia, Kotayk, (Darevsky 1967), published data; (41.9070, 43.5000), 936 m, Georgia, Achaldaba, (Murphy et al. 1996), published data; (40.6050, 43.4228), 1752 m, Turkey, Kars, (Uzzell and Darevsky 1975), published data; (40.9833, 44.6333), 1199 m, Armenia, Lori, (Darevsky 1967), published data; (40.6375, 44.5483), 2070 m, Armenia, Ankavan, (MacCulloch et al. 1995), published data; (40.7442, 44.8206), 1468 m, Armenia, Tavush, (MacCulloch et al. 1995), published data; (41.0208, 44.3817), 1418 m, Armenia, Kotayk, (MacCulloch et al. 1995), published data; (40.6867, 44.8556), 1713 m, Armenia, Tavush, (MacCulloch et al. 1995), published data; (40.3000, 43.6667), 1261 m, Armenia, Aragatsotn, (MacCulloch et al. 1995), published data; (40.9833, 44.6333), 1199 m, Armenia, Lori, (MacCulloch et al. 1995), published data; (40.7333, 44.8167), 1352 m, Armenia, Tavush, (Fu et al. 1999), published data; (40.6375, 44.5483), 2070 m, Armenia, Kotayk, (Fu et al. 1999), published data; (41.0208, 44.3817), 1418 m, Armenia, Lori, (Fu et al. 1999), published data; (40.6867, 44.8556), 1713 m, Armenia, Tavush, (Fu et al. 1999), published data; (40.3000, 43.6667), 1261 m, Armenia, Aragatsotn, (Fu et al. 1999), published data; (41.0000, 44.6700), 1226 m, Armenia, Lori, (Fu et al. 1999), published data; (41.6667, 43.5000), 2410 m, Georgia, Samtskhe-Javakheti, (Fu et al. 1999), published data; (40.2622, 46.5879), 1966 m, Nagorno-Karabakh, Tonashen, (Darevsky 1967), published data; (40.4274, 46.3922), 1507 m, Azerbaijan, Sarisu, (Darevsky 1967), published data; (40.3722, 46.0737), 1767 m, Azerbaijan, Dashkasan, (Darevsky 1967), published data; (40.5014, 45.9161), 1764 m, Azerbaijan, Dashkasan, (Darevsky 1967), published data; (40.4481, 45.5272), 2609 m, Armenia, Gegharkunik, (Darevsky 1967), published data; (40.5995, 45.4677), 1762 m, Azerbaijan, Gadabay, (Darevsky 1967), published data; (40.7217, 45.5570), 1481 m, Azerbaijan, Tovuz, (Darevsky 1967), published data; (40.8260, 45.3414), 1321 m, Armenia, Tavush, (Darevsky 1967), published data; (40.6876, 45.2928), 2440 m, Armenia, Gegharkunik, (Darevsky 1967), published data; (40.3152, 45.1142), 1988 m, Armenia, Gegharkunik, (Darevsky 1967), published data; (40.7770, 44.9330), 1131 m, Armenia, Tavush, (Darevsky 1967), published data; (41.0067, 44.8233), 1550 m, Armenia, Tavush, (Darevsky 1967), published data; (40.8519, 44.7540), 1851 m, Armenia, Lori, (Darevsky 1967), published data; (40.7441, 44.5982), 2211 m, Armenia, Lori, (Darevsky 1967), published data; (40.6311, 44.7215), 2150 m, Armenia, Kotayk, (Darevsky 1967), published data; (40.6351, 44.4753), 2093 m, Armenia, Kotayk, (Darevsky 1967), published data; (40.5866, 44.0508), 2407 m, Armenia, Shirak, (Darevsky 1967), published data; (40.7324, 44.2774), 2154 m, Armenia, Lori, (Darevsky 1967), published data; (41.0636, 44.3295), 1482 m, Armenia, Lori, (Darevsky 1967), published data; (41.1629, 44.5004), 1568 m, Armenia, Lori, (Darevsky 1967), published data; (41.2768, 44.6488), 1004 m, Georgia, Kvemo Kartli, (Darevsky 1967), published data; (41.277, 43.9078), 2744 m, Georgia, Samtskhe-Javakheti, (Darevsky 1967), published data; (41.5399, 44.108), 1543 m, Georgia, Kvemo Kartli, (Darevsky 1967), published data; (41.6204, 43.8633), 1572 m, Georgia, Kvemo Kartli, (Darevsky 1967), published data; (41.6362, 43.6461), 2027 m, Georgia, Tabatskuri, (Darevsky 1967), published data; (41.3722, 43.6114), 2049 m, Georgia, Samtskhe-Javakheti, (Darevsky 1967), published data; (41.0714, 43.0836), 2432 m, Turkey, Ardahan, (Darevsky 1967), published data; (41.0668, 42.5511), 1870 m, Turkey, Ardahan, (Darevsky 1967), published data; (41.2616, 42.6602), 2475 m, Turkey, Ardahan, (Darevsky 1967), published data; (41.0125, 44.5039), 1443 m, Armenia, Lori, (Darevsky 1967), published data; (40.8872, 44.4906), 1916 m, Armenia, Lori, (Darevsky 1967), published data; (41.0808, 44.6575), 1340 m, Armenia, Lori, (Martirosyan et al. 2003), published data; (40.9117, 44.4321), 2025 m, Armenia, Lori, (Martirosyan et al. 2003), published data; (40.9794, 44.4091), 1738 m, Armenia, Lori, (Martirosyan et al. 2003), published data; (40.4673, 45.0621), 1915 m, Armenia, Lchap, (Martirosyan et al. 2003), published data; (40.6223, 44.5809), 2142 m, Armenia, Kotayk, (Martirosyan et al. 2003), published data; (40.6125, 44.6065), 1919 m, Armenia, Kotayk, (Martirosyan et al. 2003), published data; (40.6646, 44.8901), 2121 m, Armenia, Gegharkunik, (Martirosyan et al. 2003), published data; (40.7077, 44.7622), 1785 m, Armenia, Tavush, (Martirosyan et al. 2003), published data; (40.7023, 44.6086), 2798 m, Armenia, Kotayk, (Martirosyan et al. 2003), published data; (40.5167, 44.3833), 1880 m, Armenia, Aragatsotn, (Danielyan et al. 2008), personal records up to 2018; (41.0667, 42.8333), 1922 m, Turkey, Ardahan, (Darevsky 1967), published data; (40.6167, 44.5500), 2123 m, Armenia, Kotayk, (Darevsky 1967), published data; (40.9833, 44.9500), 1674 m, Armenia, Tavush, (Darevsky 1967), published data; (40.1011, 45.9542), 2240 m, Azerbaijan, Kalbajar, (Arakelyan et al. 2011), published data; (40.1461, 45.7540), 2120 m, Armenia, Gegharkunik, (Arakelyan et al. 2011), published data; (40.3768, 45.1351), 1997 m, Armenia, Gegharkunik, (Arakelyan et al. 2011), published data; (40.8604, 45.3606), 1306 m, Armenia, Tavush, (Arakelyan et al. 2011), published data; (40.8507, 45.3188), 1600 m, Armenia, Tavush, (Arakelyan et al. 2011), published data; (40.8423, 45.2562), 1519 m, Armenia, Tavush, (Arakelyan et al. 2011), published data; (40.8961, 45.1718), 813 m, Armenia, Tavush, (Arakelyan et al. 2011), published data; (41.0078, 45.1171), 1141 m, Armenia, Tavush, (Arakelyan et al. 2011), published data; (40.8082, 44.8688), 1803 m, Armenia, Tavush, (Arakelyan et al. 2011), published data; (40.7225, 44.8647), 1452 m, Armenia, Tavush, (Arakelyan et al. 2011), published data; (40.7478, 44.8026), 1623 m, Armenia, Tavush, (Arakelyan et al. 2011), published data; (41.1772, 44.7138), 1334 m, Armenia, Lori, (Arakelyan et al. 2011), published data; (40.9649, 44.6413), 1039 m, Armenia, Lori, (Arakelyan et al. 2011), published data; (40.6732, 44.5620), 2736 m, Armenia, Kotayk, (Arakelyan et al. 2011), published data; (40.6220, 44.5448), 2177 m, Armenia, Kotayk, (Arakelyan et al. 2011), published data; (40.4511, 44.3983), 1809 m, Armenia, Aragatsotn, (Arakelyan et al. 2011), published data; (40.5949, 44.3374), 1959 m, Armenia, Aragatsotn, (Arakelyan et al. 2011), published data; (40.8249, 44.2775), 1546 m, Armenia, Spitak, (Arakelyan et al. 2011), personal records up to 2018; (40.8870, 44.1771), 1942 m, Armenia, Lori, (Arakelyan et al. 2011), personal records up to 2018; (40.8692, 43.9464), 1767 m, Armenia, Shirak, (Arakelyan et al. 2011), personal records up to 2018; (40.9157, 44.4219), 2120 m, Armenia, Lori, (Arakelyan et al. 2011), personal records up to 2018; (40.9674, 44.4282), 1495 m, Armenia, Lori, (Arakelyan et al. 2011), personal records up to 2018; (41.0016, 44.3620), 1529 m, Armenia, Lori, (Arakelyan et al. 2011), personal records up to 2018; (41.1927, 44.3187), 1635 m, Armenia, Lori, (Arakelyan et al. 2011), personal records up to 2018; (41.0442, 43.6436), 2047 m, Armenia, Shirak, (Arakelyan et al. 2011), personal records up to 2018; (41.0590, 43.6563), 2037 m, Armenia, Shirak, (Arakelyan et al. 2011), personal records up to 2018; (40.8506, 43.9595), 1756 m, Armenia, Shirak, (Arakelyan et al. 2011), personal records up to 2018; (40.8927, 44.1954), 1818 m, Armenia, Lori, (Arakelyan et al. 2011), personal records up to 2018; (40.8229, 44.2893), 1563 m, Armenia, Lori, (Arakelyan et al. 2011), personal records up to 2018; (40.9961, 44.3894), 1439 m, Armenia, Lori, (Arakelyan et al. 2011), personal records up to 2018; (40.9514, 44.44082), 1432 m, Armenia, Lori, (Arakelyan et al. 2011), personal records up to 2018; (40.9019, 44.4251), 1816 m, Armenia, Lori, (Arakelyan et al. 2011), personal records up to 2018; (40.5906, 44.3629), 1883 m, Armenia, Aragatsotn, (Arakelyan et al. 2011), personal records up to 2018; (40.4494, 44.4044), 1827 m, Armenia, Aragatsotn, (Arakelyan et al. 2011), personal records up to 2018; (40.6203, 44.56321), 1857 m, Armenia, Kotayk, (Arakelyan et al. 2011), personal records up to 2018; (40.5136, 44.9362), 1923 m, Armenia, Gegharkunik, (Arakelyan et al.

2011), personal records up to 2018; (40.3543, 45.1415), 1954 m, Armenia, Gegharkunik, (Arakelyan et al. 2011), personal records up to 2018; (40.1688, 45.7346), 1954 m, Armenia, Gegharkunik, (Arakelyan et al. 2011), personal records up to 2018; (40.7460, 44.8723), 1224 m, Armenia, Tavush, (Arakelyan et al. 2011), personal records up to 2018; (40.1256, 45.9378), 2535 m, Armenia, Gegharkunik, (Arakelyan et al. 2011), personal records up to 2018; (40.8827, 45.2846), 1166 m, Armenia, Tavush, (Arakelyan et al. 2011), personal records up to 2018; (40.8909, 45.3502), 1257 m, Armenia, Tavush, (Arakelyan et al. 2011), personal records up to 2018; (40.6546, 44.5810), 2360 m, Armenia, Kotayk, (Arakelyan et al. 2011), personal records up to 2018; (40.8954, 45.3983), 859 m, Armenia, Tavush, (Arakelyan et al. 2011), personal records up to 2018; (41.0172, 45.1373), 893 m, Armenia, Tavush, (Arakelyan et al. 2011), personal records up to 2018; (40.9700, 44.6267), 1226 m, Armenia, Lori, (Arakelyan et al. 2011), personal records up to 2018; (40.7529, 45.0013), 1418 m, Armenia, Lori, (Arakelyan et al. 2011), personal records up to 2018; (41.1740, 44.7209), 1284 m, Armenia, Lori, (Arakelyan et al. 2011), personal records up to 2018; (40.7173, 44.8702), 1587 m, Armenia, Tavush, (Arakelyan et al. 2011), personal records up to 2018; (40.0996, 44.6283), 1169 m, Armenia, Tavush, (Arakelyan et al. 2011), personal records up to 2018; (40.8020, 44.8900), 1433 m, Armenia, Tavush, (Arakelyan et al. 2011), personal records up to 2018; (40.7547, 44.8018), 1486 m, Armenia, Tavush, (Arakelyan et al. 2011), personal records up to 2018; (40.7643, 44.8881), 1319 m, Armenia, Tavush, (Arakelyan et al. 2011), personal records up to 2018; (40.8008, 44.8909), 1433 m, Armenia, Tavush, (Arakelyan et al. 2011), personal records up to 2018; (40.7159, 44.7727), 1500 m, Armenia, Tavush, (Arakelyan et al. 2011), personal records up to 2018; (40.7185, 44.7305), 1683 m, Armenia, Tavush, (Arakelyan et al. 2011), personal records up to 2018; (40.2235, 46.0046), 2113 m, Nagorno Karabakh, Sotk, (Arakelyan et al. 2011), personal records up to 2018; (40.8927, 44.1954), 1818 m, Armenia, Lori, (Arakelyan et al. 2011), personal records up to 2018; (40.6203, 44.5631), 1857 m, Armenia, Artavaz, (Arakelyan et al. 2011), personal records up to 2018; (40.6546, 44.5810), 2360 m, Armenia, Kotayk, (Arakelyan et al. 2011), personal records up to 2018; (40.7402, 44.8261), 1315 m, Armenia, Tavush, (Arakelyan et al. 2011), personal records up to 2018; (40.8020, 44.8901), 1433 m, Armenia, Tavush, (Arakelyan et al. 2011), personal records up to 2018; (40.6203, 44.5631), 1857 m, Armenia, Artavaz, (Arakelyan et al. 2011), personal records up to 2018; (40.6546, 44.5810), 2360 m, Armenia, Kotayk, (Arakelyan et al. 2011), personal records up to 2018; (41.0137, 44.3827), 1340 m, Armenia, Lori, (Arakelyan et al. 2011), personal records up to 2018; (40.0997, 44.6283), 1169 m, Armenia, Tavush, (Arakelyan et al. 2011), personal records up to 2018; (40.5399, 44.3734), 1936 m, Armenia, Aragatsotn, (Arakelyan et al. 2011), personal records up to 2018; (40.6546, 44.58102), 2360 m, Armenia, Kotayk, (Arakelyan et al. 2011), personal records up to 2018; (40.9961, 44.3894), 1439 m, Armenia, Lori, (Arakelyan et al. 2011), personal records up to 2018; (41.0012, 42.8417), 2241 m, Armenia, Ardahan, (Arakelyan et al. 2011), personal records up to 2018; (40.9462, 44.4721), 1411 m, Armenia, Lori, (Arakelyan et al. 2011), personal records up to 2018; (41.1676, 44.3220), 1634 m, Armenia, Lori, (Arakelyan et al. 2011), personal records up to 2018; (41.0136, 44.3834), 1346 m, Armenia, Lori, (Arakelyan et al. 2011), personal records up to 2018; (41.1669, 44.3274), 1689 m, Armenia, Lori, (Arakelyan et al. 2011), personal records up to 2018; (40.9382, 44.4826), 1499 m, Armenia, Lori, (Arakelyan et al. 2011), personal records up to 2018; (41.1676, 44.3220), 1634 m, Armenia, Lori, (Arakelyan et al. 2011), personal records up to 2018; (40.5352, 44.6972), 1973 m, Armenia, Kotayk, (Arakelyan et al. 2011), personal records up to 2018; (40.6902, 44.8635), 1717 m, Armenia, Tavush, (Arakelyan et al. 2011), personal records up to 2018; (40.2234, 46.0046), 2113 m, Armenia, Sotk, (Arakelyan et al. 2011), personal records up to 2018; (40.5294, 44.3880), 1922 m, Armenia, Aragatsotn, (Arakelyan et al. 2011), personal records up to 2018; (40.9462, 44.4721), 1411 m, Armenia, Lori, (Arakelyan et al. 2011), personal records up to 2018; (40.6186, 44.5639), 1855 m, Armenia, Kotayk,

(Arakelyan et al. 2011), personal records up to 2018; (40.9462, 44.4721), 1411 m, Armenia, Lori, (Arakelyan et al. 2011), personal records up to 2018; (40.7572, 44.8041), 1461 m, Armenia, Tavush, (Arakelyan et al. 2011), personal records up to 2018; (41.3937, 43.4697), 1719 m, Georgia, Samtskhe-Javakheti, (Arakelyan et al. 2011), personal records up to 2018; (41.0686, 43.6551), 2020 m, Armenia, Shirak, (Arakelyan et al. 2011), personal records up to 2018; (40.5044, 44.7485), 1700 m, Armenia, Kotayk, (Arakelyan et al. 2011), personal records up to 2018; (40.5044, 44.7483), 1700 m, Armenia, Kotayk, (Arakelyan et al. 2011), personal records up to 2018; (41.1613, 43.7943), 2116 m, Georgia, Samtskhe-Javakheti, (Arakelyan et al. 2011), personal records up to 2018; (40.6546, 44.5810), 2360 m, Armenia, Kotayk, (Arakelyan et al. 2011), personal records up to 2018; (40.8927, 44.1954), 1818 m, Armenia, Lori, (Arakelyan et al. 2011), personal records up to 2018; (41.1404, 45.0013), 1126 m, Armenia, Tavush, (Arakelyan et al. 2011), personal records up to 2018; (41.4495, 44.5832), 493 m, Georgia, Kvemo Kartli, (Arakelyan et al. 2011), personal records up to 2018; (40.7577, 44.8030), 1484 m, Armenia, Tavush, (Arakelyan et al. 2011), personal records up to 2018; (40.7564, 44.8825), 1182 m, Armenia, Tavush, (Arakelyan et al. 2011), personal records up to 2018; (40.8008, 44.8909), 1433 m, Armenia, Tavush, (Arakelyan et al. 2011), personal records up to 2018; (40.7159, 44.7727), 1500 m, Armenia, Tavush, (Arakelyan et al. 2011), personal records up to 2018; (40.7185, 44.7305), 1683 m, Armenia, Tavush, (Arakelyan et al. 2011), personal records up to 2018; (40.8532, 43.9478), 1700 m, Armenia, Shirak, (Arakelyan et al. 2011), personal records up to 2018; (41.4813, 43.2802), 1130 m, Georgia, Samtskhe-Javakheti, (Arakelyan et al. 2011), personal records up to 2018; (41.1385, 44.3961), 1738 m, Armenia, Lori, (Arakelyan et al. 2011), personal records up to 2018; (40.9851, 43.7884), 1968 m, Armenia, Shirak, (Arakelyan et al. 2011), personal records up to 2018; (41.0059, 43.9379), 2061 m, Armenia, Shirak, (Arakelyan et al. 2011), personal records up to 2018; (41.0697, 44.1122), 1830 m, Armenia, Lori, (Arakelyan et al. 2011), personal records up to 2018; (41.0039, 44.4304), 1372 m, Armenia, Lori, (Arakelyan et al. 2011), personal records up to 2018; (41.1281, 44.9194), 1235 m, Armenia, Lori, (Arakelyan et al. 2011), personal records up to 2018; (40.6955, 44.8528), 1562 m, Armenia, Tavush, (Arakelyan et al. 2011), personal records up to 2018; (40.8203, 45.1539), 1036 m, Armenia, Tavush, (Arakelyan et al. 2011), personal records up to 2018; (40.5259, 44.7648), 1702 m, Armenia, Kotayk, (Arakelyan et al. 2011), personal records up to 2018; (40.5339, 44.7162), 1893 m, Armenia, Kotayk, (Arakelyan et al. 2011), personal records up to 2018; (40.5339, 44.7046), 1902 m, Armenia, Kotayk, (Arakelyan et al. 2011), personal records up to 2018; (40.6065, 43.9997), 1978 m, Armenia, Shirak, (Arakelyan et al. 2011), personal records up to 2018; (40.6048, 44.0001), 1994 m, Armenia, Shirak, (Arakelyan et al. 2011), personal records up to 2018; (40.7513, 44.9603), 1344 m, Armenia, Tavush, (Danielyan et al. 2008), personal records up to 2018; (40.7529, 44.9619), 1340 m, Armenia, Tavush, (Danielyan et al. 2008), personal records up to 2018; (41.0299, 43.8205), 1991 m, Armenia, Shirak, (Arakelyan et al. 2011), personal records up to 2018; (41.0241, 43.8132), 1978 m, Armenia, Shirak, (Arakelyan et al. 2011), personal records up to 2018; (40.8149, 44.4959), 1311 m, Armenia, Lori, (Arakelyan et al. 2011), personal records up to 2018; (40.8144, 44.5022), 1328 m, Armenia, Lori, (Arakelyan et al. 2011), personal records up to 2018; (40.8165, 44.5005), 1307 m, Armenia, Lori, (Arakelyan et al. 2011), personal records up to 2018; (41.0898, 44.8520), 885 m, Armenia, Lori, (Arakelyan et al. 2011), personal records up to 2018; (40.5698, 45.3130), 2032 m, Armenia, Gegharkunik, (Arakelyan et al. 2011), personal records up to 2018; (40.5087, 44.4397), 1864 m, Armenia, Aragatsotn, (Arakelyan et al. 2011), personal records up to 2018; (40.5088, 44.4401), 1868 m, Armenia, Aragatsotn, (Arakelyan et al. 2011), personal records up to 2018.

D. valentini (latitude, longitude), elevation, country, province, reference, sources. (41.0167, 43.8333), 2048 m, Armenia, Shirak, (Darevsky 1967), published data; (39.7500, 43.5000), 2471 m, Turkey, Agrı, (Fu et al. 1999), published data; (41.0167, 43.8333), 2048 m, Armenia, Shirak, (Darevsky 1967), published data; (40.5080, 44.9380), 1965 m,

Armenia, Gegharkunik, (Murphy et al. 1996), published data; (38.6281, 42.2252), 2249 m, Turkey, Bitlis, (Murphy et al. 1996), published data; (39.3713, 43.9992), 2544 m, Turkey, Van, (Murphy et al. 1996), published data; (38.4661, 42.1862), 1915 m, Turkey, Bitlis, (Murphy et al. 1996), published data; (39.9918, 45.0991), 2508 m, Armenia, Ararat, (Arakelyan et al. 2011), published data; (41.0666, 42.455), 1847 m, Turkey, Ardahan, (Fu et al. 1999), published data; (40.3833, 44.7000), 1892 m, Armenia, Kotayk, (Murphy et al. 1996), published data; (40.5128, 44.9009), 1983 m, Armenia, Gegharkunik, (Martirosyan et al. 2003), published data; (40.7022, 44.6086), 2798 m, Armenia, Kotayk, (Martirosyan et al. 2003), published data; (40.3041, 44.7280), 2333 m, Armenia, Kotayk, (Martirosyan et al. 2003), published data; (40.5305, 44.2843), 2913 m, Armenia, Aragatsotn, (Martirosyan et al. 2003), published data; (40.0632, 45.5921), 2761 m, Armenia, Gegharkunik, (Uzzell and Darevsky 1975), published data; (40.0587, 45.2518), 2196 m, Armenia, Gegharkunik, (Uzzell and Darevsky 1975), published data; (40.1590, 45.1233), 2399 m, Armenia, Gegharkunik, (Uzzell and Darevsky 1975), published data; (40.2380, 45.0474), 2771 m, Armenia, Gegharkunik, (Uzzell and Darevsky 1975), published data; (40.3230, 45.0847), 2043 m, Armenia, Gegharkunik, (Uzzell and Darevsky 1975), published data; (40.3281, 44.9626), 2648 m, Armenia, Gegharkunik, (Uzzell and Darevsky 1975), published data; (40.4016, 44.9814), 2297 m, Armenia, Gegharkunik, (Uzzell and Darevsky 1975), published data; (40.3860, 44.8501), 2430 m, Armenia, Kotayk, (Uzzell and Darevsky 1975), published data; (40.4788, 44.9256), 2103 m, Armenia, Gegharkunik, (Uzzell and Darevsky 1975), published data; (40.6847, 44.5544), 2384 m, Armenia, Gegharkunik, (Uzzell and Darevsky 1975), published data; (40.6010, 44.4225), 2357 m, Armenia, Aragatsotn, (Uzzell and Darevsky 1975), published data; (40.5189, 44.2075), 3540 m, Armenia, Aragatsotn, (Uzzell and Darevsky 1975), published data; (40.5670, 44.1339), 2874 m, Armenia, Shirak, (Uzzell and Darevsky 1975), published data; (40.4096, 44.1460), 2747 m, Armenia, Aragatsotn, (Uzzell and Darevsky 1975), published data; (41.2554, 43.9948), 2521 m, Georgia, Kvemo Kartli, (Uzzell and Darevsky 1975), published data; (41.234, 43.7542), 2146 m, Georgia, Samtskhe-Javakheti, (Uzzell and Darevsky 1975), published data; (41.2293, 43.6391), 2038 m, Georgia, Samtskhe-Javakheti, (Uzzell and Darevsky 1975), published data; (40.8117, 43.1268), 1823 m, Turkey, Kars, (Uzzell and Darevsky 1975), published data; (41.1171, 42.6021), 1802 m, Turkey, Ardahan, (Uzzell and Darevsky 1975), published data; (39.9184, 45.8208), 3118 m, Azerbaijan, Zangezur Ridge, (Arakelyan et al. 2011), personal records up to 2018; (39.9002, 45.7382), 2554 m, Armenia, Vayots Dzor, (Arakelyan et al. 2011), personal records up to 2018; (40.0896, 45.4923), 2264 m, Armenia, Gegharkunik, (Arakelyan et al. 2011), personal records up to 2018; (40.0973, 45.9524), 2097 m, Nagorno Karabakh, Kalbajar, (Arakelyan et al. 2011), personal records up to 2018; (40.4072, 45.5041), 2333 m, Armenia, Gegharkunik, (Arakelyan et al. 2011), personal records up to 2018; (40.4418, 45.4687), 2273 m, Armenia, Gegharkunik, (Arakelyan et al. 2011), personal records up to 2018; (40.4750, 45.4170), 2025 m, Armenia, Gegharkunik, (Arakelyan et al. 2011), personal records up to 2018; (40.1723, 44.8201), 2186 m, Armenia, Kotayk, (Arakelyan et al. 2011), personal records up to 2018; (40.2063, 44.7800), 2139 m, Armenia, Kotayk, (Arakelyan et al. 2011), personal records up to 2018; (40.2885, 44.7657), 1934 m, Armenia, Kotayk, (Arakelyan et al. 2011), personal records up to 2018; (40.3040, 44.8195), 2254 m, Armenia, Kotayk, (Arakelyan et al. 2011), personal records up to 2018; (40.3785, 44.8688), 2548 m, Armenia, Kotayk, (Arakelyan et al. 2011), personal records up to 2018; (40.5049, 44.9164), 1979 m, Armenia, Gegharkunik, (Arakelyan et al. 2011), personal records up to 2018; (40.5589, 44.5967), 2506 m, Armenia, Kotayk, (Arakelyan et al. 2011), personal records up to 2018; (40.6649, 44.5680), 2870 m, Armenia, Kotayk, (Arakelyan et al. 2011), personal records up to 2018; (40.6177, 44.5369), 2351 m, Armenia, Kotayk, (Arakelyan et al. 2011), personal records up to 2018; (40.5476, 44.5242), 2270 m, Armenia, Aragatsotn, (Arakelyan et al. 2011), personal records up to 2018; (40.5430, 44.3658), 1960 m, Armenia, Aragatsotn, (Arakelyan et al. 2011), personal records up to 2018; (40.5886, 44.3130), 2143 m, Armenia, Aragatsotn, (Arakelyan et al. 2011), personal records up to 2018; (40.4947, 44.2327), 2731 m, Armenia, Aragatsotn, (Arakelyan et al. 2011), personal records up to 2018; (40.3938, 44.2248), 2197 m, Armenia, Aragatsotn, (Arakelyan et al. 2011), personal records up to 2018; (40.6255, 44.0492), 2073 m, Armenia, Shirak, (Arakelyan et al. 2011), personal records up to 2018; (40.5740, 44.3462), 2032 m, Armenia, Aragatsotn, (Arakelyan et al. 2011), published data; (41.0590, 43.6563), 2037 m, Armenia, Shirak, (Arakelyan et al. 2011), published data; (40.6203, 44.5631), 1857 m, Armenia, Kotayk, (Arakelyan et al. 2011), published data; (40.4920, 44.2494), 2747 m, Armenia, Shirak, (Arakelyan et al. 2011), published data; (41.0883, 43.8844), 2358 m, Armenia, Shirak, (Arakelyan et al. 2011), published data; (40.3912, 44.2342), 2151 m, Armenia, Aragatsotn, (Arakelyan et al. 2011), published data; (39.7925, 45.5430), 1821 m, Armenia, Vayots Dzor, (Arakelyan et al. 2011), published data; (40.5399, 44.3734), 1936 m, Armenia, Aragatsotn, (Arakelyan et al. 2011), published data; (40.6313, 44.0556), 2049 m, Armenia, Shirak, (Arakelyan et al. 2011), published data; (40.5413, 44.5385), 2449 m, Armenia, Kotayk, (Arakelyan et al. 2011), published data; (40.5537, 44.6059), 2787 m, Armenia, Kotayk, (Arakelyan et al. 2011), published data; (40.5136, 44.9362), 1923 m, Armenia, Gegharkunik, (Arakelyan et al. 2011), published data; (40.1256, 45.9378), 2535 m, Armenia, Gegharkunik, (Arakelyan et al. 2011), published data; (40.6546, 44.5810), 2360 m, Armenia, Kotayk, (Arakelyan et al. 2011), published data; (40.2848, 44.8360), 2450 m, Armenia, Kotayk, (Arakelyan et al. 2011), published data; (40.2677, 44.7785), 1943 m, Armenia, Kotayk, (Arakelyan et al. 2011), published data; (40.4041, 44.4498), 2314 m, Armenia, Kotayk, (Arakelyan et al. 2011), published data; (39.7328, 46.0230), 3034 m, Armenia, Syunik, (Arakelyan et al. 2011), published data; (39.6752, 46.0769), 3394 m, Armenia, Syunik, (Arakelyan et al. 2011), published data; (39.6038, 46.16303), 2858 m, Armenia, Syunik, (Arakelyan et al. 2011), published data; (39.8672, 45.7180), 2357 m, Armenia, Vayots Dzor, (Arakelyan et al. 2011), published data; (39.9166, 45.7898), 3072 m, Armenia, Vayots Dzor, (Arakelyan et al. 2011), published data; (39.9596, 45.5452), 2577 m, Armenia, Vayots Dzor, (Arakelyan et al. 2011), published data; (39.8938, 45.5954), 3092 m, Armenia, Vayots Dzor, (Arakelyan et al. 2011), published data; (40.4072, 45.5147), 2303 m, Armenia, Gegharkunik, (Arakelyan et al. 2011), published data; (40.449, 45.5075), 2540 m, Armenia, Gegharkunik, (Arakelyan et al. 2011), published data; (40.4819, 45.4824), 2585 m, Armenia, Gegharkunik, (Arakelyan et al. 2011), published data; (40.5149, 45.4285), 2548 m, Armenia, Gegharkunik, (Arakelyan et al. 2011), published data; (40.3749, 44.8903), 2727 m, Armenia, Kotayk, (Arakelyan et al. 2011), published data; (40.1417, 44.822), 1832 m, Armenia, Kotayk, (Arakelyan et al. 2011), published data; (40.1691, 44.804), 2099 m, Armenia, Kotayk, (Arakelyan et al. 2011), published data; (40.2235, 46.0046), 2113 m, Nagorno Karabakh, Sotk, (Arakelyan et al. 2011), published data; (40.6546, 44.5810), 2360 m, Armenia, Kotayk, (Arakelyan et al. 2011), published data; (40.5136, 44.9362), 1923 m, Armenia, Gegharkunik, (Arakelyan et al. 2011), published data; (40.6546, 44.5810), 2360 m, Armenia, Kotayk, (Arakelyan et al. 2011), personal records up to 2018; (40.5136, 44.9362), 1923 m, Armenia, Gegharkunik, (Arakelyan et al. 2011), personal records up to 2018; (40.5399, 44.3734), 1936 m, Armenia, Aragatsotn, (Arakelyan et al. 2011), personal records up to 2018; (40.6546, 44.5810), 2360 m, Armenia, Kotayk, (Arakelyan et al. 2011), personal records up to 2018; (40.5136, 44.9362), 1923 m, Armenia, Lchashen, (Arakelyan et al. 2011), personal records up to 2018; (40.2234, 46.0046), 2113 m, Nagorno-Karabakh, Sotk, (Arakelyan et al. 2011), personal records up to 2018; (40.5294, 44.3880), 1922 m, Armenia, Aragatsotn, (Arakelyan et al. 2011), personal records up to 2018; (40.5294, 44.388), 1922 m, Armenia, Aragatsotn, (Arakelyan et al. 2011), personal records up to 2018; (40.51088, 44.9365), 1950 m, Armenia, Gegharkunik, (Arakelyan et al. 2011), personal records up to 2018; (41.6090, 43.0863), 981 m, Georgia, Samtskhe-Javakheti, (Arakelyan et al. 2011), personal records up to 2018; (41.3937, 43.4697), 1719 m, Georgia,

Samtskhe-Javakheti, (Arakelyan et al. 2011), personal records up to 2018; (41.0728, 43.7514), 2025 m, Armenia, Shirak, (Arakelyan et al. 2011), personal records up to 2018; (40.0349, 45.2458), 2263 m, Armenia, Gegharkunik, (Arakelyan et al. 2011), personal records up to 2018; (39.8383, 45.6517), 2249 m, Armenia, Vayots Dzor, (Arakelyan et al. 2011), personal records up to 2018; (41.4495, 44.5832), 493 m, Georgia, Kvemo Kartli, (Arakelyan et al. 2011), personal records up to 2018; (41.4813, 43.2802), 1130 m, Georgia, Samtskhe-Javakheti, (Arakelyan et al. 2011), personal records up to 2018; (41.0311, 43.8299), 2011 m, Armenia, Shirak, (Arakelyan et al. 2011), personal records up

to 2018; (41.0058, 43.9379), 2061 m, Armenia, Shirak, (Arakelyan et al. 2011), personal records up to 2018; (41.0299, 43.8205), 1991 m, Armenia, Shirak, (Arakelyan et al. 2011), personal records up to 2018; (41.0241, 43.8132), 1978 m, Armenia, Shirak, (Arakelyan et al. 2011), personal records up to 2018; (39.1545, 46.0381), 2898 m, Armenia, Syunik, (Danielyan et al. 2008), personal records up to 2018; (39.9549, 45.8600), 2757 m, Azerbaijan, Kelbajar, (Danielyan et al. 2008), personal records up to 2018; (39.9479, 45.2406), 2298 m, Armenia, Gegharkunik, (Danielyan et al. 2008), personal records up to 2018.

Table A1. Environmental parameters at locations of *Darevskia armeniaca* and *D. valentini* in this study. Abbreviations: W_A=air humidity (%), T_A=air temperature (°C), T_{US}=surface temperature (°C), V_w=wind speed (m/s), H_E= elevation (m)

Species	Voucher no.	Province/locality	W _A	T _A	T _{US}	V _w	H _E
<i>D. armeniaca</i>	IEERAS 366	Kotayk/Tsaghkadzor	55	27	29	1.3	1750
<i>D. armeniaca</i>	IEERAS 367	Gegharkunik/Lchashen	46	25.4	30	1.3	1950
<i>D. armeniaca</i>	IEERAS 369	Kotayk/Megradzor	45.6	22.3	29.7	2.6	1833
<i>D. armeniaca</i>	IEERAS 370	Kotayk/YSU student camp	52.7	21.2	26.6	2.6	1832
<i>D. armeniaca</i>	IEERAS 371	Kotayk/YSU student camp	45.3	23.8	27	2.2	1830
<i>D. armeniaca</i>	IEERAS 372	Kotayk/Tutudzhur	35.7	20.3	25.6	1.9	2060
<i>D. armeniaca</i>	IEERAS 373	Kotayk/Ehribuni camp	36.7	20.1	25.3	1.2	2088
<i>D. armeniaca</i>	IEERAS 374	Tavush/Semyonovsky Mountain Pass	56.5	25.8	27.7	0.6	1578
<i>D. armeniaca</i>	IEERAS 375	Tavush/Road to Dilijan	46.5	28.5	27.8	0.4	1342
<i>D. armeniaca</i>	IEERAS 376	Tavush/Haghartsin	43.9	30	25	0.3	1443
<i>D. armeniaca</i>	IEERAS 377	Tavush/Haghartsin Monastery	46.9	26.5	32.4	0	1436
<i>D. armeniaca</i>	IEERAS 378	Kotayk/Kentron-Hrazdan	17.3	31.5	33	0	1700
<i>D. armeniaca</i>	IEERAS 379	Gegharkunik/Karabakh–Sotk road	25.9	25.7	47.8	1.7	2124
<i>D. armeniaca</i>	IEERAS 381	Aragatsotn/Kuchak	21.9	32	36	2	1920
<i>D. armeniaca</i>	IEERAS 383	Vayots Dzor/Hors	36.1	29.5	31	1.1	2080
<i>D. armeniaca</i>	IEERAS 384	Shirak/Harichavank	57.8	22.4	24.2	0.4	1993
<i>D. armeniaca</i>	IEERAS 385	Shirak/Mets Sepasar	38.3	30.7	39	0.2	1990
<i>D. armeniaca</i>	IEERAS 387	Shirak/Mets Sepasar bridge	50.5	22.7	39.5	0.2	1991
<i>D. valentini</i>	IEERAS 368	Gegharkunik/Lchashen	46	25.4	30	1.3	1950
<i>D. valentini</i>	IEERAS 380	Gegharkunik/Karabakh–Sotk road	25.9	25.7	47.8	1.7	2124
<i>D. valentini</i>	IEERAS 382	Aragatsotn/Kuchak	21.9	32	36	2	1920
<i>D. valentini</i>	IEERAS 404	Aragatsotn/Kuchak	17.9	35.1	46	2.1	1925
<i>D. valentini</i>	IEERAS 405	Aragatsotn/Kuchak	33.1	45.7	47.8	2.1	1916
<i>D. valentini</i>	IEERAS 386	Shirak/Mets Sepasar	38.3	30.7	39	0.2	1990
<i>D. valentini</i>	IEERAS 406	Shirak/Mets Sepasar	38.2	30.9	39	0.3	1990
<i>D. valentini</i>	IEERAS 388	Shirak/Sepasar bridge	50.5	22.7	39.5	0.2	1986